

POST-ALIGHTING BEHAVIOR OF *CERATITIS CAPITATA*
(DIPTERA: TEPHRITIDAE) ON ODOR-BAITED TRAPS

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ABSTRACT

The influence of physiological state on the behavior of released laboratory-cultured *Ceratitis capitata* (Wiedemann) flies was evaluated after their arrival on four commonly-used odor-baited traps hung in a potted host tree in a field cage. Three-day-old and 12-day-old protein-deprived females and males were significantly more inclined than 3-day-old and 12-day-old protein-fed females and males to enter protein-odor-baited McPhail and Heath-Epsky traps. There was little or no influence of physiological state on propensity of flies to enter trimedlure-baited Jackson or Nadel-Harris traps. Across all physiological states combined, 74, 64, 0 and 0% of arriving females entered McPhail, Heath-Epsky, Jackson and Nadel-Harris traps, respectively. Corresponding values for arriving males were 60, 59, 86 and 82%. We suggest that future research on protein-odor-baited traps should be aimed at enticing a greater proportion of alighting *C. capitata* flies to enter the trap.

Key Words: Odor response, Mediterranean fruit flies, physiological state

RESUMEN

Fue evaluada la influencia del estado fisiológico en el comportamiento de *Ceratitis capitata* (Wiedemann), criadas en el laboratorio, al llegar a cuatro trampas con cebos odoríferos. Las trampas fueron colgadas de un árbol hospedante plantado en una maceta dentro de una jaula. Las hembras y machos de 3 y 12 días de edad privados de proteína se inclinaron significativamente más a entrar en las trampas de McPhail y Heath-Epsky cebadas con proteína odorífera que las hembras y machos de la misma edad alimentados con proteína. Hubo poca o ninguna influencia del estado fisiológico en la propensión de las moscas a entrar en las trampas de Jackson o Nadel-Harris cebadas con trimedlure. A través de todos los estados fisiológicos combinados, 74, 64, 0, y 0% de las hembras que llegaban entraron a las trampas de McPhail, Heath-Epsky, Jackson y Nadel-Harris, respectivamente. Los valores correspondientes a los machos que llegaban a las trampas fueron 60, 59, 86 y 82%. Sugerimos que en el futuro debe investigarse sobre trampas cebadas con proteína odorífera que permitan atraer hacia su interior a una mayor proporción de *C. capitata* que se posen sobre ellas.

The Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), is a major pest of fruit and vegetables on several continents. Numerous studies have been conducted evaluating the effectiveness of a wide variety of traps for detecting *C. capitata* adults (Cunningham 1989; Economopoulos 1989; Economopoulos & Haniotakis 1994; Katsoyannos 1994; Millar 1995). The most commonly used traps employ either trimedlure (a synthetic parapheromone) as a male attractant or protein hydrolysate (a food-type lure) as an attractant for both sexes (Liquido et al. 1993). Typically, *C. capitata* response to trap stimuli is evaluated on the basis of total number of flies captured per trap. Only a few studies have distinguished, through direct behavioral observation or otherwise, between the number of *C. capitata* arriving nearby or upon a trap and the proportion of arrivers actually captured (Prokopy & Economopoulos 1975; Villeda et al. 1988; Hendrichs et al. 1989; Liquido et al. 1993). Observed variation in proportion of attracted flies caught could have been due to variation in trap characteristics, the structure of the habitat in the immediate vicinity of a trap, weather conditions or the physiological state of responding flies.

Here, in a potted host tree in a field cage, we evaluated the influence of fly physiological state on the proportion of *C. capitata* alighting on a trap that eventually was captured. Specifically, we examined four physiological states of released females and males (immature or mature, protein-deprived or protein-fed) and four types of protein-baited or trimedlure-baited traps.

MATERIALS AND METHODS

C. capitata used in all trials originated from a laboratory colony in culture at the USDA Tropical Fruit and Vegetable Research Laboratory in Honolulu for about 100 generations. From eclosion until time of release, females and males were held together in 30 × 30 × 30 cm screened cages supplied with sucrose and water, with or without protein (enzymatic yeast hydrolysate). Holding conditions were about 25°C, 50% RH and 13 h natural daylength. Flies were tested when 3 days old (females immature and males of unknown maturity) or 12 days old (females and males mature). Immature females lacked fully developed eggs whereas mature females carried an average of 38 or 125 fully developed eggs per female according to whether they did not or did receive protein. Being immature, 3-day-old females were presumed to be un-

mated; being mature, 12-day-old females were presumed to be mated. Females and males of the same class were released into the lower center of a non-fruiting potted guava tree whose canopy was about 1 m diam. The field cage containing the tree was located on the grounds of the USDA laboratory in Honolulu and was protected from direct sunlight and rainfall by an opaque tarpaulin above the ceiling. For each release event, we collected about 10 female and about 10 male flies of the same class in glass vials and allowed the flies to crawl from the tip of a vial onto the surface of leaves. Immediately following release of a batch of about 20 flies, we hung a trap in the upper third of the tree canopy. Batches of about 20 flies were released until a total of 25 flies of both sexes combined (=one replicate) alighted on or in a trap, at which time a trap of a different type was tested.

Trap types evaluated were: (a) a 16-cm-diam clear glass invaginated bell-shaped McPhail trap baited with a 200 ml liquid solution of 9% Nulure (Miller Chemical Co., Hanover, PA) (a proteinaceous food-type attractant), 5% sodium borate and 86% water (depicted in Katsoyannos 1994); (b) a Phase-2 Heath-Epsky green-colored plastic cylindrical (10 cm diam \times 15 cm tall) dry trap baited on the interior with single dispensers of ammonium acetate and putrescine and three evenly-spaced 22-mm-diam entry holes midway between the top and bottom of the trap (flies that entered were killed by contact with squares of methomyl-impregnated waxed cardboard affixed to the top and bottom interior of the trap) (Heath & Epsky 1995); (c) a white cardboard Jackson dry trap (delta shaped) with a white sticky basal insert, baited with a trimedlure impregnated polymeric plug (AgriSense Ltd., Fresno, CA) and placed in a basket hung at the top center of the trap interior (depicted in Katsoyannos 1994); and (d) a clear plastic Nadel-Harris lid-covered bucket trap baited with a trimedlure-impregnated plug (as in c) placed in a basket hung at the top center of the trap interior with three evenly-spaced 22-mm holes entry holes at the upper third of the trap wall (entering flies were killed by the fumigant action of a naled dispenser on the floor of the trap) (depicted in Katsoyannos 1994). Exterior surfaces of all traps were washed before use.

Each fly that alighted on the exterior of a trap or flew directly to the trap interior was observed. Observations continued until the fly either was captured or killed (by drowning, sticky, or insecticide) or left the trap without being captured or killed. For each type of trap we carried out a total of four replicates (total of 100 alighting flies) for each of the four physiological states tested. Trap types and fly types were evaluated in random order. All flies that remained in the cage after completion of a replicate of a treatment were removed before the next treatment commenced.

RESULTS

Across all four fly physiological-state classes combined, 74, 64, 0 and 0% of arriving females entered McPhail, Heath-Epsky, Jackson and Nadel-Harris traps, respectively. Corresponding values for arriving males were 60, 59, 86 and 82%.

Across the four physiological-state classes of flies arriving on McPhail traps, 68-80% were females and 20-32% were males (Table 1). Comparable values for flies arriving on Heath-Epsky traps were 56-64% females and 36-44% males. In contrast, across the four physiological states of flies arriving on Jackson and Nadel-Harris traps, 0-6% were females and 94-100% were males. Because we released approximately, not precisely, 10 females and 10 males at each release event, statistical comparison among trap types of the proportion of individuals of each sex released that arrived on a trap was considered invalid.

With respect to females, a significantly greater proportion of arrivers that were protein-deprived than protein-fed entered both McPhail and Heath-Epsky traps (Ta-

TABLE 1. PROPORTION OF LABORATORY-CULTURED RELEASED *C. CAPITATA* FLIES ARRIVING AT A TRAP THAT ENTERED THE TRAP.

Sex	Fly age (days)	Protein	Mean No. Arriving Flies and Mean % Arrivers that Entered Traps ¹											
			McPhail Trap			Heath-Epsky Trap			Jackson Trap			Nadel-Harris Trap		
			No. Arrive	% Enter	No. Arrive	% Enter	No. Arrive	% Enter	No. Arrive	% Enter	No. Arrive	% Enter		
Female	3	Deprived	17.8	87a(a)	16.0	69b(b)	1.0	0a(c)	1.0	0a(c)	1.0	0a(c)		
	3	Fed	20.0	72b(a)	13.8	56c(b)	0.8	0a(c)	1.5	0a(c)	1.5	0a(c)		
Male	12	Deprived	19.5	85a(a)	14.3	81a(a)	0.3	0a(b)	0.5	0a(b)	0.5	0a(b)		
	12	Fed	16.8	51c(a)	15.8	48c(a)	0.0	0a(b)	0.3	0a(b)	0.3	0a(b)		
	3	Deprived	7.3	72a(b)	9.0	73a(b)	24.0	87ab(a)	24.0	87ab(a)	24.0	77a(ab)		
	3	Fed	5.0	53b(b)	11.3	48b(b)	24.3	93a(a)	23.5	93a(a)	23.5	86a(a)		
	12	Deprived	5.5	68a(b)	10.8	70a(b)	24.8	83ab(a)	24.5	83ab(a)	24.5	84a(a)		
	12	Fed	8.3	48b(b)	9.3	46b(b)	25.0	81b(a)	24.8	81b(a)	24.8	79a(a)		

¹For each sex, values in the same column not followed by the same letter without parentheses, or values in the same row not followed by the same letter within parentheses, are significantly different from one another according to one-way ANOVA (following arc-sine transformation) and the least significant difference test criterion at the 0.05 level. For each sex, values in each cell for ANOVA consisted of the proportion of arriving flies that entered the trap. There were four replicates per treatment.

ble 1). This was true for both ages of females tested. Among all four classes of females tested, arriving 12-day-old protein-fed individuals were the least inclined to enter McPhail or Heath-Epsky traps. No arriving females entered a Jackson or Nadel-Harris trap. A significantly greater proportion of arriving 3-day-old protein-deprived and protein-fed females entered McPhail traps than Heath-Epsky traps, but there were no significant differences between these two traps in proportion of arriving 12-day-old females that entered a trap (Table 1).

With respect to males, again, a significantly greater proportion of protein-deprived than protein-fed flies entered both McPhail and Heath-Epsky traps (Table 1). This was true for both age classes of flies tested. Again, among all four classes of males tested, arriving 12-day-old protein-fed individuals were the least inclined to enter McPhail or Heath-Epsky traps. The proportion of arrivers that entered a Jackson or Nadel-Harris trap varied little according to class of males tested (Table 1). Almost without exception, a significantly greater proportion of males arriving on Jackson or Nadel-Harris traps than on McPhail or Heath-Epsky traps entered the trap (Table 1).

No female or male that arrived at a McPhail, Heath-Epsky or Nadel-Harris trap entered the interior of the trap without first landing on the exterior and then walking into the interior. In contrast, 53-59% of arriving males flew directly into the interior of Jackson traps.

Of flies that entered the interior of traps, percentages that were captured (did not escape) were as follows for McPhail, Heath-Epsky, Jackson and Nadel-Harris traps, respectively: 96-98, 89-93, 86-92 and 95-99.

DISCUSSION

Our findings indicate that for all four classes of released laboratory-cultured *C. capitata* flies combined, about 74, 60, 2, and 3% of flies attracted to McPhail, Heath-Epsky, Jackson and Nadel-Harris traps, respectively, were females (we released approximately equal numbers of females and males). If the total number of female and male arrivers on a given trap type is multiplied by the proportion of each sex arriving that entered the trap (again for all four fly classes combined), then the percentage of all female flies released that entered a trap and was female turns out to be 78, 62, 0 and 0, respectively, for the four types of traps. These values parallel quite closely the proportions of all natural-population *C. capitata* captured that were females in field studies with Nulure-baited McPhail traps (71%) (Katsoyannos 1994), ammonium acetate/putrescine-baited Heath-Epsky traps (53%) (Heath & Epsky 1995), trimedlure-baited Jackson traps (0%) (Katsoyannos 1994), and trimedlure-baited Nadel-Harris traps (0%) (Katsoyannos 1994). Thus, even though we were unable to obtain and test wild-origin *C. capitata*, our combined findings across four physiological states of laboratory-cultured *C. capitata* tested under field cage conditions are similar (with respect to sex ratio of responding flies) to findings for wild *C. capitata* obtained under field conditions.

Our findings revealed a significant effect of protein diet on proportions of arriving flies that entered McPhail and Heath-Epsky traps. Indeed, for all four comparisons involving 3-day or 12-day-old protein-deprived versus protein-fed females or males, the response of arrivers to protein-type odor emanating from the interior of McPhail traps was always significantly greater on the part of protein-deprived flies. The same was true for Heath-Epsky traps. On the other hand, in only one of the four comparisons for both the McPhail and Heath-Epsky traps was the response different between 3-day and 12-day-old flies, suggesting that the protein diet rather than fly age had a greater effect on propensity of alighting flies to enter traps containing protein-type

lures. Effects of female age per se may have coincided with effects of mating status on female response patterns in that 3-day-old females were presumed to be unmated and 12-day-old females were presumed to be mated. Our study, however, was not designed to distinguish between effects of age and mating status. Earlier, it was found that protein-deprivation was more important than fly age on degree of attraction of wild-origin *C. capitata* to sources of protein in a field-caged tree (Prokopy et al. 1992).

Katsoyannos (1994) observed that significantly more natural-population *C. capitata* females were captured in protein-baited McPhail traps than in trimedlure-baited Jackson or Nadel-Harris traps, whereas the reverse was true for male medflies. Heath & Epsky (1995) found that on average across several experiments, numerically (but not always significantly) more natural-population *C. capitata* of both sexes combined were captured in McPhail traps than in Heath-Epsky traps. Here, a significantly greater proportion of arriving 3-day-old protein-deprived and protein-fed females entered McPhail traps than traps of any other types, while a significantly greater proportion of arriving males of all types (except 3-day-old protein-deprived ones) entered Jackson and Nadel-Harris traps than McPhail or Heath-Epsky traps. Perhaps difference in medfly captures among trap types tested by Katsoyannos (1994) and Heath & Epsky (1995) stemmed in part from differential attraction towards, and differential post-alighting behavior at, respective sources of trap odor according to the physiological state of responding flies.

In conclusion, we have shown that the physiological state of *C. capitata*, with respect to amount of protein consumed in life and to a lesser extent fly age, can have a significant impact on the propensity of flies attracted to a protein-odor-baited trap to enter the trap. Perhaps certain characteristics or practices associated with current protein-odor baited traps could be adjusted to facilitate entry of flies of all physiological states into traps following their arrival on or near the trap.

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